

THE RUBIACEOUS GENUS MUSSAENDA: THE MORPHOLOGY OF THE ASIATIC SPECIES

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THE RUBIACEOUS genus *Mussaenda* comprises some 190 species distributed in a broad band extending through the Old World tropics from Africa and Madagascar to India and Ceylon, China, Malaysia, the Philippines, Polynesia, New Guinea, and Australia. The group includes several valuable ornamental shrubs and is of considerable biological interest, both because of the unusual development of one or more of the calyx lobes into large, colorful, petaloid structures and because of the presence of heterostyly (associated with differences in pollen size) in every species of the genus. Although a number of hybrids have been produced in the Philippine Islands using a "double" form in which all of the sepals are petaloid, nothing seems to be known of the breeding mechanisms, other biological features, or chromosome numbers within the genus.

Various taxonomic and floristic studies have treated parts of the genus, but *Mussaenda* has not been monographed since 1830 when only 27 species were known to A. P. de Candolle. At the present time, the large number of species involved, the paucity of herbarium materials, the difficulty of establishing specific characters, and the lack of opportunity for field studies of live plants make an approach on a regional basis most feasible. Accordingly, the present paper is a general survey of morphological variation in the genus, especially as represented in Asia. This will be followed by taxonomic treatments of the species of various areas, the two papers to follow immediately dealing with those of India and Ceylon and of the Philippine Islands.

A number of morphological characteristics have been used in the classification of species of *Mussaenda*. De Candolle (1830) distinguished three sections (no longer tenable) on the basis of the presence or absence of the expanded petaloid calyx segments, the number of leaves at each node, and the persistence or deciduousness of the calyx segments on the fruit. In connection with Asiatic species, J. D. Hooker (1880), Gamble (1921), Ridley (1923), Kurz (1877), and Pitard (1923) based their classifications on a combination of characters of the inflorescence, calyx lobes, corolla tube, and the pubescence and venation of the leaves. Wernham (1913) suggested a character of the stipule to be important in treating *Mussaenda* in Africa. Valetton (1925) used leaf characteristics in classifying the species of New Guinea. Bremekamp (1940) has stressed the extent of hairiness inside the corolla tube, the nature of the stipules, the presence or absence of floral dimorphism, the insertion of the stamens, and the nature of the pubescence in determining relationships between the Rubiaceae in

general, but such a study has not been made for *Mussaenda*, *sensu lato*.

Since 1916 a number of segregate genera, none of which is included in the present consideration of *Mussaenda*, have been proposed. Wernham (1916) established *Pseudomussaenda*, basing it on the African *M. luteola* Del. and including *M. monteiroi* Wernh., *M. capsulifera* Balf. f., and a new species *P. gossweileri*, and stated that "the character of the fruit of this plant certainly suffices to remove it not only from the genus *Mussaenda*, but also from the tribe Mussaendeae in spite of its resemblance in habit to other species of that genus." In 1939, Ridley raised *Mussaenda* sect. *Asemanthia* to generic rank, stating that this name was first "proposed by Stapf for a number of plants originally described as belonging to the genus *Mussaenda* but differing in the large size of the corolla and in the absence of the white phyllomorphic calyx lobes so conspicuous in that genus." Assigning the Malayan and Bornean *M. mutabilis* Hemsl., *M. spectabilis* Ridley, and *M. coccinea* Stapf, and a new species *A. lobbii* Ridley to the group, he suggested that species from tropical Africa possessing these same characters should be transferred here.

In 1937, Bremekamp proposed that the genus *Aphaenandra* Miquel, based on a Sumatran plant, be recognized to include two species, *A. uniflora* (*Acranthera uniflora* Kurz, *Aphaenandra sumatrana* Miq., *Mussaenda uniflora* Wall. ex G. Don, *M. theifera* Pierre) and *A. parva* (*M. parva* Wall. ex G. Don, *M. sootepensis* Craib, *M. neosootepensis* Craib). These species are herbaceous, (10–20 cm. tall), spread by runners, and have a terminal dichasium with stout monochasial branches reduced to two or three flowers, with parts resembling those of *Mussaenda* except for the dehiscence of the fruit.

Finally, in 1948, Li proposed the genus *Schizomussaenda* to include *Mussaenda dehiscens* Craib (*Greenea hoensis* Pierre ex Pitard, *Schizophragma macrosepalum* Hu, *Emmenopteris rehderi* Metcalf). Li did not discuss the relationship of his new genus with the earlier *Pseudomussaenda*, and the differences between them do not seem to be sufficient to warrant a distinction.

The validity of these generic segregates is beyond the scope of the present paper and will be considered at a later time. Hence, generic synonymy has been omitted here, and the generic description and notes on morphology given here are based on the Asiatic species of *Mussaenda*, *sensu stricto*.

Herbarium specimens were obtained on loan from the following institutions for which the standard abbreviations cited are used in the text.

- A Arnold Arboretum of Harvard University, Cambridge, Massachusetts.
- BSI Herbarium, Botanical Survey of India, Poona.
- C Botanical Museum and Herbarium, Copenhagen.
- GH Gray Herbarium of Harvard University, Cambridge, Massachusetts.
- K Herbarium, Royal Botanic Gardens, Kew.
- LWG Herbarium, National Botanic Gardens, Lucknow.
- NY Herbarium, New York Botanical Garden.

PNH Philippine National Herbarium, Manila.
US U. S. National Herbarium, Washington.

I wish to take this opportunity to thank the directors and curators of the institutions named above for allowing me to examine the specimens under their care. I wish also to thank in particular Dr. Richard A. Howard, under whose supervision and guidance this investigation was conducted, and Dr. Lily M. Perry, for her unfailing interest and encouragement. Mrs. Lazella Schwarten, librarian of the Arnold Arboretum and Gray Herbarium, was of immense help to me in tracing pertinent literature, and Drs. Bernice G. Schubert and C. E. Wood, Jr., have contributed materially in their editorial capacities. Further, I wish to express my appreciation and deep gratitude to the Rockefeller Foundation, for grant of scholarship funds during this period, and to the Arnold Arboretum, for a Mercer Fellowship.

Mussaenda Linnaeus, Sp. Pl. 1: 177. 1753; Gen. Pl. ed. 5. 82. 1754.¹

Erect or scandent shrubs or undershrubs, rarely herbs; stems branching, glabrous or pubescent; bark thin, gray or brown, lenticellate and firm or papery, peeling off in flakes. Leaves opposite or ternately whorled, petiolate, unequal, membranous, large or small, lanceolate to ovate or obovate, entire, glabrous or hairy, the upper surface less hairy, more hairy on the usually prominent veins below, apex acute or obtuse, long or short acuminate, base long or short cuneate, equilateral or inequilateral, acute, obtuse, rounded or sometimes subcordate; petioles varying in length, thin or stout, pubescent or glabrous. Stipules interpetiolar, caducous or persistent, large or small, membranous or thick, ovate to lanceolate or oblong, opposite pairs sometimes fusing at their bases forming a ring round the node, pubescent outside, glabrous or pubescent and with glands inside, with 2 or more pairs of branching vascular strands, the apex acuminate, acute and entire or bifurcate, the base expanded laterally within the petiolar bases. Inflorescences terminal and from the axils of the terminal pair of leaves, large or small, spreading or compact, few to many flowered, dichotomous or trichotomous cymose corymbs. Flowers small to large, heterostylous, bisexual, and radially symmetrical, sessile or pedicellate. Bracts and bracteoles deciduous, linear to ovate, glabrous or pubescent, bracteoles usually trifid or trilaciniate. Calyx tube oblong to turbinate, lobes 5, small or large, triangular, linear, subulate, lanceolate to obovate or foliar, deciduous or persistent, glabrous or pubescent inside and/or outside with one or more pairs of glands at the base of each lobe, vascular strands usually 3, the 2 laterals sometimes branching at their bases; one lobe in some flowers often transformed to a large, petaloid, white to yellowish appendage or sometimes all five petaloid.

¹The first collection of the genus was made by Paul Hermann, chief medical officer in the Dutch East India Company, in Ceylon, between 1672 and 1677, and he gave it the vernacular name "Mussaenda." Hermann's plant was described by Burmann in his *Thesaurus Zeylanicus* (1737), and the name was then adopted by Linnaeus, the plant becoming *Mussaenda frondosa* L., the type species of the genus.

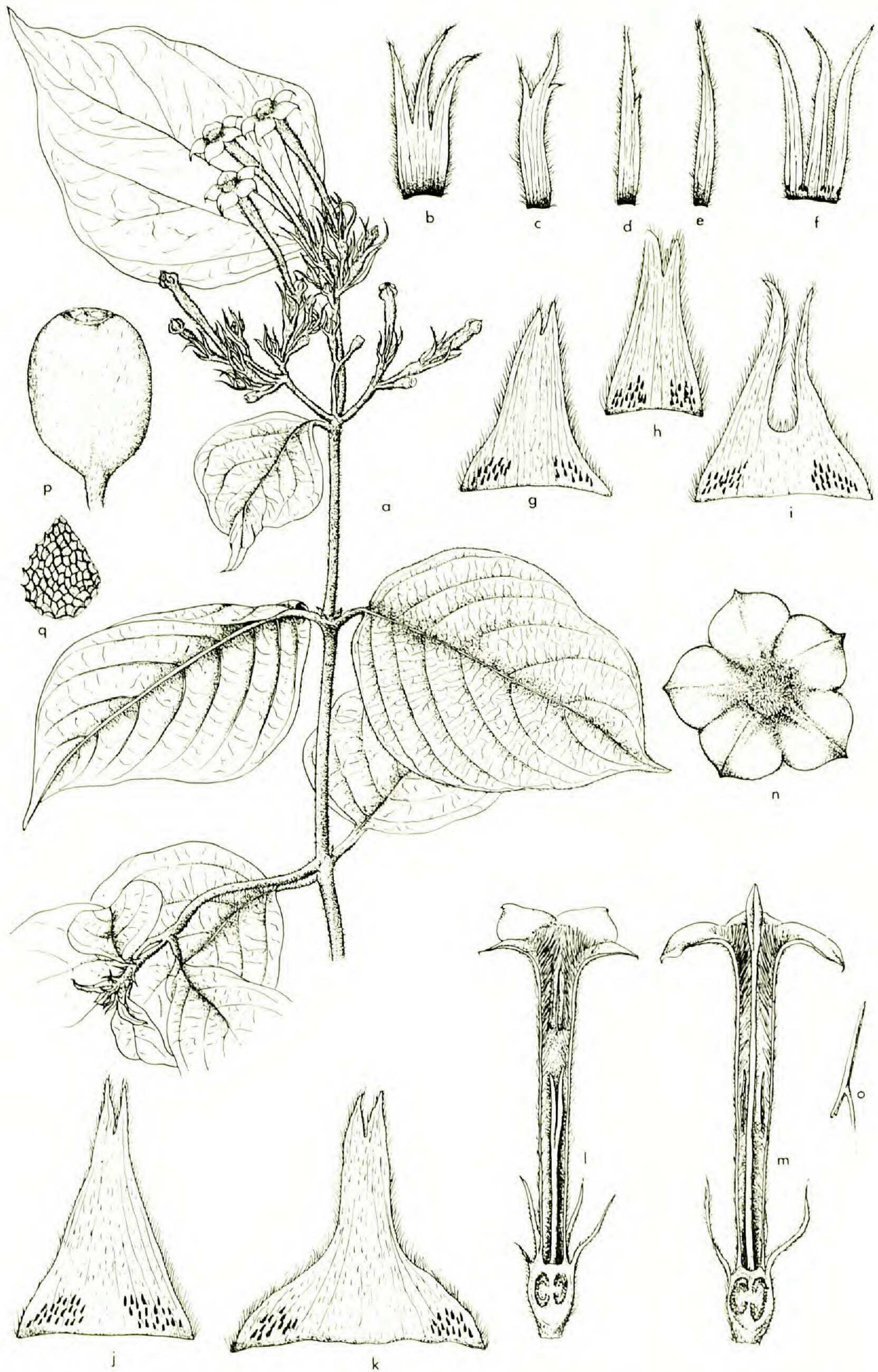


FIG. 1. *Mussaenda frondosa*: (sketches from a series of collections by the author) *a*, branch with inflorescence and petaloid sepal; *b-d*, bracteoles; *e*, bract; *f*, calyx lobes viewed from within to show glands at their bases; *g-k*, stipules spread out and viewed from the adaxial surface showing degree of bifurcation at apex and glands at base; *l*, longitudinal section of short-styled

Corolla salverform, the tube white to greenish yellow, cylindrical, or infundibuliform, broader at the top, short or long, glabrous or hairy outside and inside, hairiness varying according to the length of the style and stigma, in short-styled forms with longer hairs at the throat and between stamens and in long-styled forms with short hairs, hairiness extending as far as the bases of anthers or shortly and scantily beyond, sometimes as far as the base of the tube; hairs usually strap shaped, but if globular becoming linear and longer below the stamens; corolla lobes 5, yellow to orange-red, small or large, thick or thin, linear to lanceolate to orbicular, acute, obtuse or rounded, apiculate or caudate, glabrous or hairy outside and inside, hairs papillate by extensions of gradually shortening mouth hairs along the midline. Stamens 5, sessile or with short filaments, epipetalous towards the middle or top of the tube, never protruding beyond; anthers linear, dorsifixed, introrse, acute or obtuse at the apex, sterile and bilobed at the base, the lobes diverging, protandrous, pollen sacs dehiscent longitudinally; pollen grains usually of two sizes, those from short-styled flowers larger than those from long-styled forms. Ovary inferior, hairy or glabrous, obconical, fusiform, or cylindrical, 2-loculed with numerous ovules on fleshy, peltate, axile placentae; style long or short (heterostylous), filiform or stout, arising from the middle of a fleshy, circular, nectariferous disc, sometimes grooved on opposite sides, very rarely pubescent; stigma bilobed, long or short, the lobes diverging or firmly appressed on their papillate, receptive surfaces. Fruit a berry, short, ellipsoid, globular or long-cylindrical, glabrous or pubescent, sometimes lenticellate, with or without a crown of persistent calyx segments; seeds numerous, minute, smooth or spiny, reticulate, black or brown, triangular, oblong or ovate, embedded in a fleshy pulp; testa areolate with a varying number of foveae in the minute areoles; endosperm present; germination epigeal.

HABIT. Species of *Mussaenda* grow in a variety of climatic and environmental conditions from sea level up to an elevation of about 2000 m., along river banks, sandy river beds, in sloping ravines, and at the edge of the tropical jungles which merge into grassy, savanna slopes. They seem to prefer a well-drained, clayey or gravelly, humic soil. Most are low or medium-sized shrubs which assume a climbing or scandent habit at the edge of the jungle, so that various collectors have referred to climbing shrubs, scandent shrubs, semiwoody climbers or lianas. A few species which are vines or small trees also occur, so that the habit is not a very reliable character taxonomically.

flower with tufted hairs at mouth and stamens in throat of the corolla tube; *m*, longitudinal section of long-styled flower with tufted hairs at mouth and stamens about halfway on the corolla tube; *n*, corolla from above; *o*, dorsifixed anther with short filament and bilobed base; *p*, berry showing nectariferous gland on top and scars left by the deciduous calyx segments; *q*, seed, showing reticulations, foveae within reticulations omitted. *a* $\times \frac{1}{2}$, *b-f*, *l-n*, *p*, $\times 1\frac{1}{2}$; *g-k*, $\times 4-6$; *o*, $\times 3$; *q* $\times 15$.

Some species prefer the shade of the thick jungle, but the majority flourish in the semishade with opportunity for extending their branches over the neighboring shrubs and at the same time flanking the open side of the jungle, displaying their colorful "bracts."

The stem is woody, lenticellate, often brittle with considerable pith in the center. Young stems are glabrous or covered with whitish or reddish-brown pubescence.

LEAVES. The leaves are very variable in their form as well as in their pubescence. The two leaves at a node are usually unequal in size and in the length of petioles. Younger leaves are smaller and more pubescent than older ones. Even on the glabrate leaves scattered hairs may be found along the veins but are more frequent on the lower surface. The pubescence on the leaves and the stem is also variable in the length of the hairs, their placement, density, and location. In some species (*Mussaenda wrayi* King, *M. hirsutissima* Hutch. ex Gamble) the hairs are long and more or less at right angles to the surface of the leaf and stem, but in others, though long, they are appressed to the surface, becoming a felt-like mixture with other shorter hairs. In still other species, the hairs are very short and appressed to the surface (*M. laxa* Hutch. ex Gamble, *M. calycina* Wall.). Even the "glabrous" species are hairy in some part or other, especially in the mouth of the corolla tube or on the stipules. Variations in the shape of the apex and base of the leaf even in the same species are very considerable, while the number of pairs of lateral veins in smaller leaves is less than in the larger ones in the same plant. The petiole is short (*M. sanderiana* Ridley, *M. incana* Wall.) or long (*M. scratchleyi* Wernh., *M. benguetensis* Elmer), characteristically thick (*M. lanata* C. B. Robins., *M. whitei* S. Moore) or thin (*M. ridleyana* Wernh., *M. aestuarii* K. Schum.). Usually the base of the lamina is cuneate (*M. laxa*, *M. scratchleyi*) or acuminate-decurrent (*M. attenuifolia* Elmer, *M. treutleri* Stapf), rarely distinct from the petiole.

STIPULES. The stipules are somewhat characteristic in many species of the genus. Bases of the stipules at a node extend laterally into and are overlapped by the bases of petioles. They may extend farther and fuse so as to form a ring round the node, as in *Mussaenda keenanii* Hook. f. They are rarely completely glabrous on both surfaces, and the pubescence varies in the length of the hairs, intensity, and location. Stipules nearing complete glabrousness but with a band of hairs along the midline outside (*M. ridleyana*) and also the margin (*M. aestuarii*) are encountered in some species, while in others they may be completely glabrous inside but hairy outside (*M. glabra* Vahl, *M. incana*, *M. macrophylla* Wall. [Philippine variety], *M. keenanii*, etc.). Stipules are completely hairy on both surfaces (*M. treutleri*, *M. lanata*, *M. whitei*) or hairy outside and inside at the base only (*M. glabrata* Hutch. ex Gamble, *M. hirsutissima*, *M. vidalii* Elmer, *M. setosa* Merr., *M. scratchleyi*, *M. pilosissima* Valetton, *M. aestuarii*). In a few species (*M. benguetensis*, *M. multibracteata* Merr.)

they are completely hairy outside, and inside at the apex and base only.

The size, shape and bifurcation at the apex of stipules vary. The stipules are large (*Mussaenda keenanii*, *M. corymbosa* Roxb.) or small (*M. glabra*, *M. frondosa* L., *M. parryorum* Fischer), acute or acuminate, mostly bifurcate at the apex while in a few the apex is entire or faintly bifid (*M. magallanensis* Elmer, *M. chlorantha* Merr., *M. ridleyana*). The bifurcation of the stipule may extend up to $\frac{1}{4}$ — $\frac{1}{3}$ of the way (*M. albiflora* Merr., *M. lanata*), $\frac{1}{3}$ — $\frac{1}{2}$ of the way (*M. setosa*, *M. philippica* A. Rich., *M. vidalii*, *M. laxa*), more than halfway or almost to the base (*M. palawanensis* Merr., *M. scandens* Elmer, *M. hirsutissima*, etc.). The lobes of these divisions are usually subulate, straight on the stem or diverging, a character used by Gamble in the classification of some of the Indian mussaendas.

The distribution of glands on the stipule is a character which has not been exploited previously. The number of glands varies from few to many, usually in paired groups, or may be continuous at the base. *Mussaenda glabra*, *M. palawanensis*, *M. cylindrocarpa* Burck, *M. variolosa* Wall., etc., have few glands at the bases of stipules, while in others they are numerous. The two groups of glands run into each other and form a continuous band in certain species (*M. roxburghii* Hook. f., *M. keenanii*, *M. corymbosa*, *M. anisophylla* Vidal, *M. erosa* Champ., *M. pilosissima*).

The ontogeny and structure of the comparable glands have been worked out by Mitra (1948) for *Paederia foetida* L. and *Ixora parviflora* Vahl. The glands are periclinal divisions in the subepidermal layer, appearing as protuberances. Each gland has a central core consisting of several rows of elongated cells and a peripheral layer of palisade-like cells at right angles to it. These glands contain mucilaginous and resinous secretions.

The stipules are traversed by two to eleven pairs of vascular strands. The smaller stipules possess two or three pairs of veins (*Mussaenda philippica*, *M. scandens*), while the larger ones (*M. corymbosa*, *M. keenanii*, *M. anisophylla*) bear about five to nine pairs which are branched.

INFLORESCENCES. The type of inflorescence can easily be used to distinguish certain species, such as *Mussaenda uniflora* Hutch. & Dalz., with one to three large flowers, and *M. roxburghii*, *M. corymbosa*, and several others with the flowers condensed into heads or contracted cymes. In other species the inflorescences are spread out or diffuse (*M. philippica*, *M. laxiflora* Hutch., etc.). The presence or absence of hairs in the inflorescences and the hair-color are also striking characters. The hairs may be short and closely appressed (*M. glabra*) or long and spreading, giving a grizzled appearance as in *M. hirsutissima*, *M. wrayi*, *M. multi-bracteata*, and *M. pilosissima*. They are grayish white, brown, or reddish brown in color.

The form and nature of bracts and bracteoles are not discussed here as it is felt that their contribution is not significant owing to their variability. However, they range from large to small, lanceolate to

ovate, and glabrous to pubescent, and are normally caducous. Bracteoles are usually trifold or trilaciniate.

CALYX. The calyx consists of a tube which is fused with the ovary, only the terminal segments emerging above the junction, though a portion of the tube may still be visible joining the segments together at the top of the ovary. These calyx segments are of considerable importance in the classification of the species. They vary from minute, triangular stubs less than 0.5 mm. in length (*Mussaenda bammleri* Valetton) to large, expanded white petaloid segments resembling so-called "bracts" (*M. pentasemia* Fischer, *M. anomala* Li, *M. philippica* var. *aurorae* Sulit). The sepals vary in length, shape, thickness, and pubescence, and each sepal carries at the base one or more pairs of glands. The number of pairs of glands seems to be characteristic of certain species. Several species (such as *M. frondosa*, *M. glabra*, *M. incana*, *M. lanata*, *M. multibracteata*, *M. scandens*, *M. chlorantha*, *M. grandifolia* Elmer, *M. acuminatissima* Merr.) bear one pair of glands at the base of each sepal, while others (such as *M. macrophylla*, *M. treutleri*, *M. roxburghii*, *M. albiflora*, *M. vidalii*, *M. nervosa* Elmer, *M. anisophylla*) bear two pairs of glands. Still others (such as *M. keenanii*, *M. corymbosa*, *M. benguetensis*) carry three pairs, and four or more pairs are borne by species such as *M. philippica* and *M. oreadum* Wernh. The number of glands does not seem to be a very reliable character to be used alone, for the number varies even on individual sepals of the same flower. Hairiness of the sepals, too, does not seem to be constant. Sepals of *M. frondosa*, for instance, are always hairy outside but glabrous inside or occasionally hairy inside as well.

Each sepal is usually supplied by three vascular strands, the middle strand arising as an extension of five alternating vascular bundles in the wall of the ovary, which is supplied by ten strands. Branches from the middle strands unite with branches of adjacent vascular bundles to form the lateral strands of the sepal, and these may branch further in certain species (FIG. 2). In broader-sepaled species transverse or arched intervascular connections unite these vascular strands (*Mussaenda macrophylla*, *M. multibracteata*).

COROLLA. The corolla tube is narrow and tapering or sometimes infundibuliform, usually broadening above the point of attachment of the stamens and varying in length from 1.1 cm. (*Mussaenda lanata*) to over 6 cm. (*M. pluviatilis* S. Moore). In most species the corolla tube is pubescent outside, the hairs extending onto the outside of the petals but towards the base becoming shorter and scantier, so that in some species the tubes are almost glabrous at the base. The corolla tubes are entirely glabrous in a few species, such as *M. corymbosa*, *M. cylindrocarpa*, and *M. scratchleyi*. In some species the hairs are short and appressed, while in others they are long and directed forwards or horizontally (*M. macrophylla*, *M. multibracteata*, and *M. vidalii*).

Hairiness inside the tube appears to be associated with heterostyly in

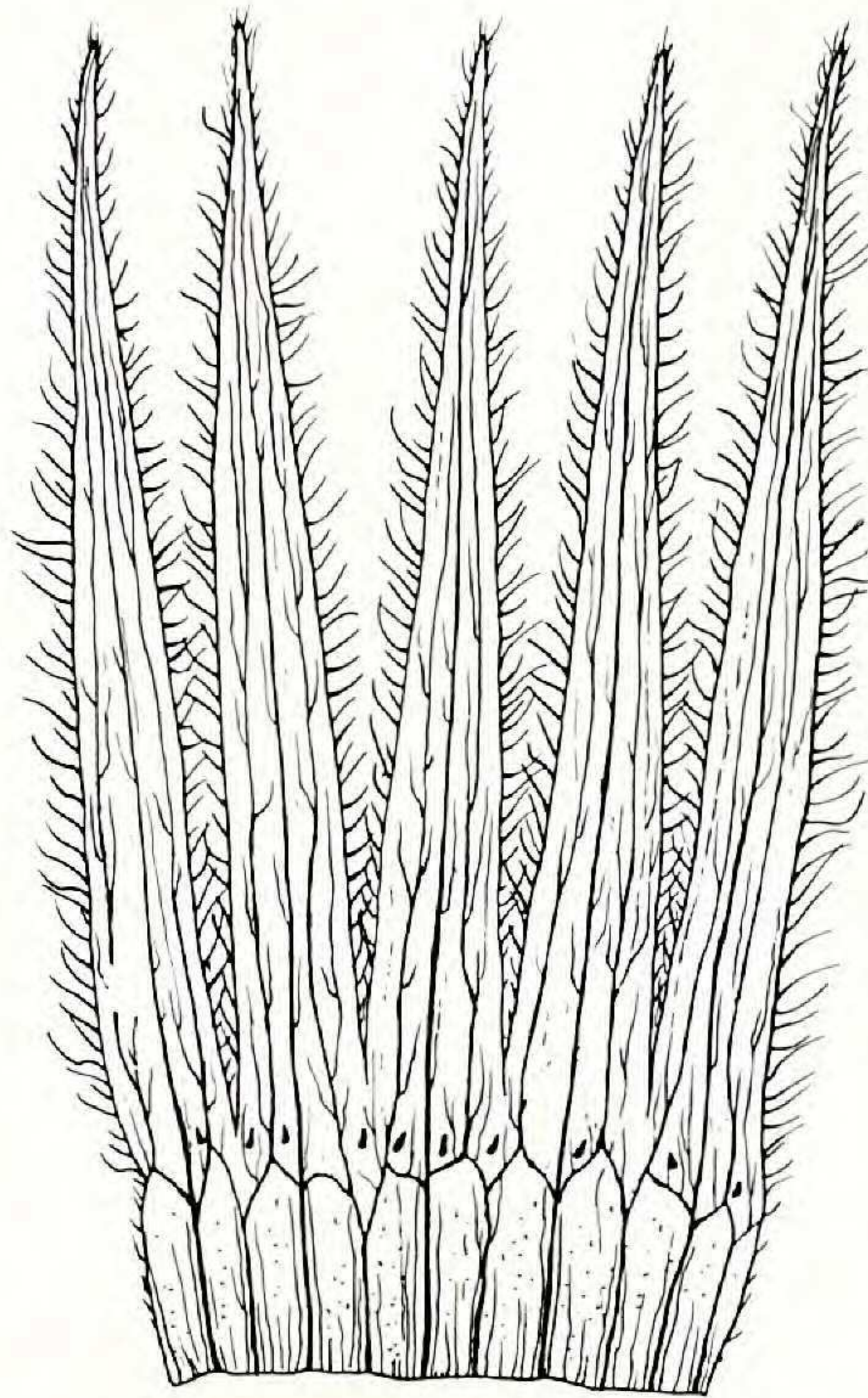


FIG. 2. Calyx lobes of *Mussaenda frondosa* together with a portion of ovary wall spread out to show vascular distribution and glands, $\times 5$.

this genus and offers characteristics of morphological and taxonomic interest. Long-styled forms usually bear shorter hairs (0.16–0.5 mm. long) than in short-styled forms (hairs inside 1.2–2 mm. long), except in the *Mussaenda frondosa* group. In all Indian mussaendas they are tufted at the mouth of the tube, a feature not observed in the Philippine and New Guinea species. Hairs are absent from inside the tube in the long-styled forms of *M. grandifolia*, except for a few short ones at the base of the corolla lobes. Elmer (1906) in describing this species says, "Corolla yellow, 3 cm. long, tubular, broadest across the top, exterior pubescent, lanose on the interior." However, the type collection was examined by me and found to be glabrous inside. In *M. ridleyana* the hairs are long, stiffish, and tapering. Hairs in the long-styled forms of species such as *M. aestuarii* and *M. oreadum* are globular (0.16 mm. long) extending as far as the base of anthers, becoming longer (0.26 mm. long), linear, and strap shaped lower down in the tube, which is glabrous at the base. Hairiness inside the tube generally extends as far as the base of the anthers or a little lower, but in certain species it extends to $\frac{1}{2}$, $\frac{3}{4}$, $\frac{4}{5}$, $\frac{9}{10}$, or the entire length of the tube. Species such as *M. roxburghii* are not only completely hairy inside but also possess a tufted ring of hairs at the base, a very useful specific character.

The corolla lobes vary in size, shape, and color (yellow to orange-red). They are lanceolate to ovate or suborbicular (broader than long) in the Indian and Philippine species, except in *Mussaenda albiflora*, the lobes of which are linear. The species of New Guinea, on the other hand, show a larger range of variations. In these the corolla lobes may be oval (*M.*

oreadum), obovate (*M. aestuarii*), oblong-lanceolate (*M. ridleyana*), or oblong (*M. ferruginea* K. Schum., etc.). They are hairy outside, and glabrous or covered with papillate hairs inside.

ANDROECIUM. The stamens are epipetalous, all attached at the same level in a ring, the position of which varies from below the middle to the top portion of the tube. They are inclosed in the tube and never protrude beyond the mouth. Hairs in the throat extend between anthers. The free portions of the filaments are very short (1–3 mm. long) (or are absent in exceptional cases, such as *Mussaenda oreadum* and *M. aestuarii*), adhere to the tube through their entire length, but exceptions in which they become free for a short distance have been observed in *M. macrophylla* (Philippine material) and several others. The dorsifixed anther is linear, short or long, acute or obtuse at the apex; the base is bilobed, with the sterile lobes rounded and appressed or diverging. The anthers are generally longer in short-styled forms than in long-styled forms. In some specimens of the long-styled forms examined the anthers do not appear to shed their pollen (*M. glabra*, Parkinson 1692; *M. scratchleyi*, Clemens 523), possibly an evolutionary tendency towards functional dioecism.

GYNOECIUM. The ovary is obconical, oblong or cylindrical, hairy or glabrous, and somewhat smaller in the short-styled forms. The wall is supplied by ten vascular bundles which branch at the bases of the sepals, supplying them with vascular strands but at the same time forming a continuous ring at the top. The style arises from the center of a nectariferous disc located at the top of the ovary. The style usually disappears in the fruit, but in a few it persists as a pointed structure (a distinguishing feature of *Mussaenda attenuifolia*). In all species the styles and stigmas of long-styled forms extend as far as the mouth of the corolla tube and lie surrounded by long, linear, strap-shaped hairs, while those of short-styled forms are much reduced and do not grow beyond the anthers. Extreme reduction is shown in some of the Javanese forms of *M. glabra*. The proportion of stigma to style varies from species to species. Stigmas over 1 cm. in length were observed in *M. grandifolia* (Edano 77424), *M. benguetensis* (Loher 1523), *M. cylindrocarpa* (Sigafos 97), and *M. aestuarii* (Brass 3896), while the stigma in *M. pluviatilis* (Brass 24306) was very small, though its style was over 6 cm. long. A style pubescent at the top was observed for the first time in the genus in *M. oreadum* from New Guinea (Brass 32073).

FRUIT AND SEED. The fruit is a fleshy berry which varies in size, shape, and pubescence. In *Mussaenda parryorum* it is less than 1 cm. long, while in *M. pluviatilis* it is over 3 cm. in length. It may be oval, ellipsoid, clavate, cylindrical, or fusiform, pubescent or glabrous, smooth or rugose, with or without lenticels. The calyx may be persistent on the fruit or deciduous leaving conspicuous scars behind. The seeds, too, vary in size and shape. They are usually very small, numerous, varying in length from about 0.5 mm. to over 1 mm., attached to cushion-shaped, fleshy placentae.

The only instance where they are embedded in the placental cushion is in *M. parryorum*, a fruit of which may contain about 80 seeds, while the normal number of seeds in a fruit of *Mussaenda* exceeds several hundred. The seeds of species such as *M. keenanii*, *M. roxburghii*, and *M. laxa* are small (0.36–0.76 mm. long), while in others (*M. incana*, *M. treutleri*, *M. hirsutissima*) they are comparatively larger (0.9–1.16 mm. long). They are minute, somewhat plump, reticulate, oval, oblong, broadly ovate, pyriform or triangular in shape. The testa is made up of an irregular network of minute ridged areas or areoles which are foveolate. This foveolate character of the areoles of the testa was used by Bremekamp (1952) to group some genera of the Rubiaceae together into closely related tribes. The number of foveae in the areoles of the testa in some species is less than in others. There is a range of overlapping limited by a fixed maximum for each species. The seeds of *M. grandifolia* bear 1–4 foveae in the testa areoles, while those of *M. lanata*, *M. anisophylla*, *M. griffithii* Wight, etc., bear 3–6 foveae. A greater number of foveae (4–12) are borne in seeds of *M. chlorantha*, *M. magallanensis*, *M. nervosa*, etc., while the largest number (5–18) occurs in *M. parryorum*. *Mussaenda glabra*, however, bears seeds with two distinct numbers of foveae (2–7 and 3–14) in the areoles of the testa. The significance of this is not yet clear. The points at which the areolar ridges meet in the seed are usually raised, but in some species, such as *M. glabrata* and *M. scandens*, these points develop into conspicuous spines. The hilum is located at the narrow end of the seed or at the back. The characters of the fruit and seed discussed above are of diagnostic value.

HETEROSTYLY. In the preceding discussion mention has been made of long-styled and short-styled flower types. Burck (1883) appears to have been the first botanist to report a heterostylous condition for *Mussaenda* when he discussed some species cultivated at Buitenzorg (Bogor). More recently, Baker (1958) noted the occurrence of this condition in some species in Ghana. The many taxonomists who have described species of *Mussaenda* have usually given detailed measurements on the length of the style, the position of the anthers, and the nature of the hairs in the throat of the corolla, but apparently not one has been aware of the heterostyly in this genus. It was apparent in the Asiatic specimens available for this study that some "species" differed only in their style-anther relationships. In the random collections assembled only a few species were not represented by both long-styled and short-styled forms. In extreme examples the long-styled forms had styles exceeding those of short-styled flowers on a ratio of 12 to 1. The average ratio appeared to be between 3 and 5 to 1. A few species showed no major difference in style length, but the length of the stigmas was in contrast between the two types.

The following tabulation (TABLE I) reports the length in millimeters of the style, stigma, ovary, and anther respectively for long-styled (L. S.) and short-styled (S. S.) flowers for species from India and Ceylon, the Philippines, and New Guinea.

TABLE I. Comparative Floral Dimensions of Long-styled and Short-styled Forms of Some Asiatic Species of *Mussaenda*

	STYLE	STIGMA	OVARY	ANTHER
India and Ceylon				
M. CORYMBOSA				
L. S. (<i>Bot. Gard. Calcutta</i>)	20	3.5	4.5	5
S. S. (<i>Kamphovener 954, Galathea Exped.</i>)	12.5	3	2.5	4.5
M. FRONDOSA				
L. S. (<i>Jayaweera, Ceylon</i>)	18-21	2.5-4	3-4	4.5-5.5
S. S. " "	13-15	3	3-3.7	5-5.5
L. S. (<i>Anglade, Kodaikanal</i>)	23	3	3.5	5.6
S. S. (<i>Bot. Gard. Calcutta</i>)	13.5	5	3.3	5.6
M. GLABRA				
L. S. (<i>Masters, Assam</i>)	14	5.5	3	5
S. S. (<i>Voigt, Calcutta</i>)	7	3	2.5	5.5
M. HIRSUTISSIMA				
L. S. (<i>Gamble 11393, Madras</i>)	23.5	1.8	3	4.2
S. S. (<i>Barnes 120, Travancore</i>)	11	2.5	4.5	6.5
M. INCANA				
L. S. (<i>Voigt 136, Calcutta</i>)	20	2.5	3.2	4.2
S. S. (<i>Hook. f., Assam</i>)	13	2	3	4
M. LAXA				
L. S. (<i>Barnes 403, Madras</i>)	29	3.5	4	6
S. S. (<i>Gamble 20541, Madras</i>)	16.5	4.5	4.5	6
M. MACROPHYLLA				
L. S. (<i>Parry 274, Assam</i>)	23	3.5	3.5	5
S. S. (<i>Belcher 145, Assam</i>)	14	3.5	4	5.7
M. ROXBURGHII				
L. S. (<i>Jenkins 496, Assam</i>)	20	3	3	5
S. S. (<i>Juan 178, Assam</i>)	13.5	2.5	3	5
M. TREUTLERI				
L. S. (<i>Gamble 9565, Sikkim</i>)	27	4	2.5	5
S. S. (<i>Hook. f. & Thomson 20, Assam</i>)	14	4.5	4	5.5
Philippine Islands				
M. ACUMINATISSIMA				
L. S. (<i>Ramos 33133, Luzon</i>)	20	7	5	4.5
M. ALBIFLORA				
L. S. (<i>Dias 29885, Negros</i>)	20	6.5	3	3.5
S. S. (<i>Ramos & Edano 31107, Panay</i>)	3	3	4	4
M. ANISOPHYLLA				
L. S. (<i>Elmer 17481, Luzon</i>)	22	9	4.5	5.5
S. S. (<i>Merrill 2508, Luzon</i>)	4	2	4.5	6.5
M. BENGUETENSIS				
L. S. (<i>Loher 1523, Cult. Trinidad</i>)	22	12	5	5

TABLE I (Continued)

	STYLE	STIGMA	OVARY	ANTHER
S. S. (<i>Santos 5497</i> , Mountain Prov.)	2.5	1.5	5	7
M. GRANDIFOLIA				
L. S. (<i>Edano 77424</i> , Palawan)	22	10	4.5	4-4.2
M. LANATA				
L. S. (<i>Merrill 1768</i> , Luzon)	7	5	3.5	3
S. S. (<i>Elmer 6195</i> , Luzon)	1.6	1.8	4	4
M. MAGALLANENSIS				
L. S. (<i>Merrill 986</i> , Mindoro)	16	6.5	3.5	3.7
S. S. (<i>Elmer 124551</i> , Sibuyan)	1.5	1.5	3.2	3
M. MULTIBRACTEATA				
L. S. (<i>Convocar 2820</i> , Luzon)	17	9	5	4.5
S. S. (<i>Ramos & Edano 28783</i> Luzon)	3	2.5	4.5	5
M. NERVOSA				
L. S. (<i>Elmer 10510</i> , Mindanao)	17	8.5	4.5	6.5
S. S. (<i>Ramos & Edano 26422</i> , Luzon)	14.5	2	4	7.5
M. PALAWANENSIS				
S. S. (<i>Ebalo & Conklin</i> , Palawan)	4	2.5	4.7	6
M. PHILIPPICA				
L. S. (<i>Ramos 30452</i> , Catanduanes)	20	6	3.5	5
S. S. (<i>Sulit & Conklin 16840</i> , Mindoro)	2.5	2.5	4.5	6.5
M. PHILIPPINENSIS				
L. S. (<i>Sulit & Conklin 17652</i> , Mindoro)	19	6.5	3.5	4
S. S. (<i>Sulit 18877</i> , Luzon)	4	3.5	4.5	5.7
M. SCANDENS				
L. S. (<i>Elmer 11291</i> , Mindanao)	13	6	3.5	3.5
S. S. (<i>Wenzel 3354</i> , Surigao)	4	2.5	3	4.5
M. VIDALII				
L. S. (<i>Elmer 11309</i> , Mindanao)	17	6	4	5.6
S. S. (<i>Ramos & Edano 39035</i> , Mindanao)	2.5	2	3.5	5
New Guinea				
M. AESTUARIII				
L. S. (<i>Brass 3896</i> , Dieni)	23	17	13	6.7
S. S. (<i>Brass 3947</i> , Dieni)	6	5	1.5	7
M. CYLINDROCARPA				
L. S. (<i>Hort. Bogor 416</i> , cult.)	9	6.5	8.5	3.2
S. S. (<i>Brass 7346</i> , Papua)	9	3.5	9	3.5
M. CYLINDROCARPA var. TOMENTOSA				
L. S. (<i>Sigafoos 97</i> , Sentani Lake)	11	9	5	4
S. S. " "	4.5	3	5	5.8

TABLE I (Continued)

	STYLE	STIGMA	OVARY	ANTHER
M. OREADUM				
L. S. (<i>Carr 14801</i> , Boridi)	25	8.5	7	5.5-7.5
S. S. (<i>Brass 5040</i> , Mt. Tafa)	9	4.5	7.5	9
M. PILOSISSIMA				
L. S. (<i>Womersley & Millar 7880</i> , Morobe Dist.)	21	7	6.5	7.5
S. S. (<i>Brass 32492</i> , Morobe Dist.)	4	2.5	4.5	4.5
M. PLUVIATILIS				
L. S. (<i>Brass 1401</i> , New Guinea)	54.5	1.5	8	7.5
L. S. (<i>Brass 24306</i> , Peria Creek)	60	2	13.5	6.5
M. PROCERA				
L. S. (<i>Brass 3276</i> , Nakeo Dist.)	19	7	5.5	5
S. S. (<i>Carr 11037</i> , New Guinea)	4	2	4	5.5
M. RIDLEYANA				
S. S. (<i>Brass 13065</i> , New Guinea)	6.2	2	4-4.5	6-7
M. SCRATCHLEYI				
L. S. (<i>Brass 5333</i> , Mafulu)	16	5	4.5	5.5
S. S. (<i>Clemens 523</i> , Morobe Dist.)	7.5	2.7	3	6
M. WHITEI				
L. S. (<i>Brass 11682</i> , Balim River)	21-23	6.5-7	5	6.5-7

In the flowering plants heterostyly represents a functionally dioecious condition. In *Mussaenda* this is apparently true of all the species examined. There is also some indication that, given time, a heterostylous condition will lead to actual dioecism or unisexual flowers. In *Mussaenda* the reduction in the length of the style from long-styled forms to short-styled forms has brought about a small but corresponding reduction in the length of the stigma and the ovary. Short-styled flower types tend to have slightly longer anthers than do long-styled flower types. A few long-styled flower forms examined do not appear either to shed or to form pollen. In short-styled flower forms there appears to be a reduction in the number of ovules developed and a tendency for the stigmatic lobes to remain appressed by their receptive surfaces in fully mature condition. A comprehensive field study of living plants is necessary to determine whether there is a tendency in either long-styled or short-styled flowers toward a greater sepal development into petaloid structures. Likewise, no information can be obtained from herbarium specimens whether one flower or the other tends to produce more fruit or a greater number of seeds.

The type of pubescence inside the corolla tube appears to be correlated with the style length. With the exception of a group of species related to *Mussaenda frondosa*, the short-styled forms tend to have longer throat hairs than do the long-styled ones. As Baker has already suggested, the throat hairs of the short-styled forms may well cause visiting insects

to struggle for entrance to the nectar-bearing area and thereby cause them to collect more pollen. In long-styled forms the insects would leave accumulated pollen on the diverging stigma lobes before approaching the area of throat hairs. Tentatively, there appear to be five types of hairs and pubescence in the corolla tubes of *Mussaenda* species. As listed below, these may well serve as a means of grouping species for further study.

The hairs in the corolla throats of the different species of *Mussaenda* can be divided into the following categories:

- (1) Long, linear, strap-shaped hairs in the throat of both long-styled and short-styled forms, e.g., the *M. frondosa* group, *M. pluvialis*, etc.
- (2) Long, linear, strap-shaped hairs in the short-styled forms and short, strap-shaped hairs in the long-styled forms, e.g., *M. glabra*, *M. philippinensis* Merr., *M. philippica*, etc.
- (3) Long, linear, strap-shaped hairs in the short-styled forms and short, globular hairs in the long-styled forms, e.g., *M. aestuarii*.
- (4) Long, stiffish, tapering hairs in the throat of short-styled forms (long-styled forms not seen), e.g., *M. ridleyana*.
- (5) Hairs absent in the throat of long-styled forms (short-styled forms not seen), e.g., *M. grandifolia*.

SUMMARY

The present study has attempted to show the range of variation to be expected in the parts normally used in taxonomic descriptions of *Mussaenda* and the relative value of each. Heterostyly is recognized as general in the genus, hence the exerted stigmas or length of the style prove of little value in limiting species. Homostylous forms have not been encountered in the specimens studied. A great many observations need to be made on living plants to aid in a future monograph.

Several groups of characteristics not used by previous students of the group are suggested as of potential value. These include the nature of the glands inside the stipules, the types of hairs found in the throat of the corolla, and the sculpturing of the seeds. The morphological characteristics which appear to be of greatest taxonomic usefulness are:

Habit (herb, shrub, or tree).

Type of inflorescence and number and distribution of flowers.

Presence or absence of petaloid sepals.

Type of fruit (dry capsule, berry, or fleshy capsule).

Number and distribution of glands inside the stipules.

Type of hairs inside the corolla tube.

Presence or absence of hairs on the style.

Size, number, and ornamentation of the seeds.

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ROYAL BOTANIC GARDENS,
PERADENIYA, CEYLON